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Citation for published version:

House, CM, Bleakley, BH, Walling, CA, Price, TAR, Stamper, CE & Moore, AJ 2011, 'The influence of maternal effects on indirect benefits associated with polyandry', *Proceedings of the Royal Society B-Biological Sciences*, vol. 278, no. 1709, pp. 1177-1182. <https://doi.org/10.1098/rspb.2010.1676>

Digital Object Identifier (DOI):

[10.1098/rspb.2010.1676](https://doi.org/10.1098/rspb.2010.1676)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Proceedings of the Royal Society B-Biological Sciences

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The influence of maternal effects on indirect benefits associated with polyandry

Clarissa M. House, Bronwyn H. Bleakley[†], Craig A. Walling[‡],
Thomas A. R. Price, Clare E. Stamper and Allen J. Moore*

Centre for Ecology and Conservation, Biosciences, College of Life and Environmental Sciences,
University of Exeter, Cornwall Campus, Penryn, Cornwall TR10 9EZ, UK

Despite numerous and diverse theoretical models for the indirect benefits of polyandry, empirical support is mixed. One reason for the difficulty in detecting indirect benefits of polyandry may be that these are subtle and are mediated by environmental effects, such as maternal effects. Maternal effects may be especially important if females allocate resources to their offspring depending on the characteristics of their mating partners. We test this hypothesis in the burying beetle *Nicrophorus vespilloides*, a species that provides extensive and direct parental care to offspring. We used a fully factorial design and mated females to one, two, three, four or five different males and manipulated conditions so that their offspring received reduced (12 h) or full (*ca* 72 h) maternal care. We found that average offspring fitness increased with full maternal care but there was no significant effect of polyandry or the interaction between the duration of maternal care and the level of polyandry on offspring fitness. Thus, although polyandry could provide a mechanism for biasing paternity towards high quality or compatible males, and variation in parental care matters, we found no evidence that female *N. vespilloides* gain indirect benefits by using parental care to bias the allocation of resources under different mating conditions.

Keywords: burying beetles; indirect benefits; maternal effects; *Nicrophorus vespilloides*; parental care; polyandry

1. INTRODUCTION

Mating can be costly to females because of increased exposure to disease, predation and/or physical harm from males. All else being equal, females should only mate as many times as necessary to gain sufficient sperm to guarantee the successful fertilization of their ova [1,2]. Yet, mating with multiple partners (polyandry) and mating repeatedly with the same partner is taxonomically widespread [1,3,4]. Multiple mating has even led to male traits that chemically [5] or physically [6] manipulate females to prevent remating. Clearly, all else is not equal and there must be factors other than fertilizing eggs driving the evolution of polyandry. Adaptive explanations for the evolution of polyandry either invoke direct benefits, where females benefit either by minimizing the cost of persistent male courtship, or by obtaining male resources that increase female fitness, or invoke indirect benefits, where females obtain genes from males that elevate offspring fitness [3]. Where females obtain direct benefits (such as nuptial gifts or hormonal stimulants in the ejaculate), or where female fitness is limited by the availability of viable sperm supplies, the evolution of polyandry presents no major theoretical problem [7]. By contrast, theoretical models of indirect benefits are diverse and controversial and empirical evidence for indirect benefits of polyandry within a species

inconclusive [3]. Various studies report a positive relationship between polyandry and offspring fitness, and invoke indirect benefits, but equally as many studies show no net effect of polyandry [1,3]. Some have even shown substantial direct [8–13] and indirect costs [11,14,15]. Thus, the question of whether polyandry generally arises from indirect benefits has yet to be resolved.

It is possible that indirect benefits of polyandry are subtle and dependent on environmental influences [7]. One potential environmental effect is maternal acquisition and allocation of resources to offspring. The amount and quality of resources that a mother provides to eggs and offspring are known as maternal effects, which influence development time and size at adulthood [16–18]. In some organisms, females differentially allocate more resources to offspring when mated to an attractive male [19], or bias allocation as reproductive compensation for her mate [3,14,20,21]. If polyandry provides a possible mechanism for females to ensure that a high-quality mate sires at least some of her offspring, then postnatal maternal effects would allow them to invest more heavily in these offspring and amplify indirect benefits.

The burying beetle *Nicrophorus vespilloides* provides a system in which to test the possibility that postnatal maternal effects influence the indirect benefits of polyandry. These beetles locate small vertebrate carcasses, which they prepare (i.e. remove the fur or feathers and roll the carcass into a ball) and bury. When the larvae arrive at the carcass, they feed on the carrion and are also fed by one or both parents. Parental care is extensive, and parents regurgitate pre-digested carrion directly into begging offspring as well as pre-digest areas of the carcass

* Author for correspondence (a.j.moore@exeter.ac.uk).

[†] Present address: Department of Biology, Stonehill College, Easton, MA, USA.

[‡] Present address: Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, UK.

that the offspring access for food. Parents also maintain the carcass, keeping it free of bacteria and fungi, and protect the carcass from intruders (reviewed in [22,23]). Variation in the care provided by a parent influences offspring growth and development, and so there are known maternal effects associated with parenting in burying beetles [24–29]. Parental care has an especially strong effect on larval survival and growth during the first 12 h [28–30]. Although reproduction is confined to a carcass, females may mate up to 70 times a day [31] on and remote from a carcass. This is comparable to the mating frequencies that have been observed in the laboratory with females mating three to four times per hour [32]. Males clearly benefit from an increased mating frequency, particularly through sperm competition [31,33] but there are limited direct benefits to females [34]. Females show an increase in fecundity, egg mass and offspring hatching success from two compared with a single mating, but these differences do not depend on whether mating is with the same or different males and do not continue past two [32,34]. This pattern reflects males transferring insufficient sperm during a single mating. Furthermore, repeated mating with the same male confers no known indirect benefits to offspring [32]. Currently, the potential for indirect benefits of polyandry for females are unknown.

We examined the relationship between polyandry and indirect benefits for females mediated through maternal effects. We conducted a manipulative experiment, where we varied the levels of polyandry and the duration of maternal postnatal care. First, if the indirect benefits of polyandry were important, we predicted that at higher levels of polyandry average offspring fitness would increase [3,15]. Second, if polyandry increases the likelihood that females mate with a high quality or compatible male(s) and therefore allocated more resources to their offspring, we predicted an interaction between maternal effects and the level of polyandry.

2. MATERIAL AND METHODS

(a) *Experimental animals*

The burying beetles used in this experiment were derived from a natural population collected in Cornwall, UK. We trapped more than 100 *N. vespilloides* in Kennel Vale Woods in September 2007 to form a genetically diverse stock population. In the laboratory, we maintained all beetles at a constant room temperature of $20 \pm 1^\circ\text{C}$ with a 16 L : 8 D photoperiod. Field-caught females were placed in individual breeding chambers ($17 \times 12 \times 6$ cm transparent, plastic container) filled with 2 cm of moist soil and a mouse carcass (Livefoods Direct Ltd, UK). We removed and froze females that successfully reared a brood when the larvae dispersed from the carcass. At this time, we also removed the dispersed larvae from the breeding chamber and housed them in individual transparent, plastic containers ($8 \times 8 \times 3.5$ cm) filled with 2 cm of soil. We recorded generation, maternal identifier and offspring identifier on the offspring's container and in a studbook, so that we knew the genealogy of each individual and purposefully outbred stocks. At eclosion, we fed each virgin F_1 offspring two decapitated mealworms (*Tenebrio*) twice a week. We used these offspring for our experiment, which commenced once the adults reached sexual maturity (16 days post-eclosion).

(b) *Experimental design*

We used a two-way factorial design to investigate the influence of number of mates and extent of parental care on offspring performance and fitness. We experimentally manipulated the number of males that mated with each female (one, two, three, four or five) to investigate the potential indirect genetic benefits for polyandrous females. We also manipulated the extent of parental care offspring received. Under one rearing regime (reduced care), larvae received 12 h of maternal care, whereas under the other rearing regime (full care), larvae received maternal care until they dispersed from the carcass (*ca* 72 h maternal care; [35]). We know from previous experiments that larvae which receive only 12 h of care develop less well and gain less mass than those that receive full care, but can survive [28,29].

At each level of polyandry, we planned a minimum sample size of 40 replicate females. Within each level of polyandry, we assigned half of each 12 h care and the other half full care. All treatments were assigned at random to females before they were initiated. Thus, the actual numbers of replicate females was slightly higher as an excess of females were setup in each treatment in the anticipation of brood failure. Final sample sizes were: one mating, 12 h care = 26; one mating, full care = 23; two matings, 12 h care = 21; two matings, full care = 21; three matings, 12 h care = 23; three matings, full care = 24; four matings, 12 h care = 24; four matings, full care = 22; five matings, 12 h care = 21; five matings, full care = 22. All analyses were performed on family means of offspring traits to avoid pseudoreplication. We did not manipulate copulation number independently of mate number; however, we know that repeated mating (i.e. several matings with the same male) does not improve any measure of offspring fitness [32]. Thus, because of our previous studies, we were confident that any effect of polyandry would not be confounded with numbers of matings.

(c) *Mating procedure*

A virgin female was mated to a single male or polyandrously to two, three, four or five virgin males in mating chambers ($11 \times 11 \times 3$ cm) (see House *et al.* [32] for details of the mating behaviour). Our previous work shows that for the single male treatment, it is necessary for females to mate more than once to obtain full fertility [32]. Thus, these females were enclosed with their mate for 50 min, during which time a pair copulates three times or more. For all polyandrous matings, females were allocated male mates that were genetically unrelated to each other or the female. Females were placed in individual mating chambers followed by a single male. All pairs were observed until the end of copulation when the male was removed from the chamber and discarded. At least 20 min separated each mating and all copulations were completed on the same day.

(d) *Maternal care and brood size manipulation*

Following mating, females were placed in a breeding chamber. Carcasses with masses ranging from 7.9 to 17.9 g were used, with 90 per cent between 9.4 and 14 g. Carcass mass was not statistically significantly different between full or partial care treatments ($F_{1,225} = 0.094$, $p = 0.760$), or between mating number treatments ($F_{4,221} = 0.633$, $p = 0.639$); nevertheless, we included carcass mass as a covariate. Breeding boxes were checked morning and evening for the presence of newly hatched larvae on the carcass. The number of larvae was counted to determine family size 12 h after the appearance of the first larvae on the carcass. Between 10 and 15 larvae were randomly selected and returned to the

crypt, the depression in the carcass where larvae feed. Family size, which has a natural range of 10–42 on this size carcass [36], was limited to a maximum of 15 larvae to minimize the effect of competition for resources on offspring phenotype [26–29]. Each brood was then assigned to one of the two treatments: full care treatment (with an adult female present when returned) or reduced care treatment (adult female present for the first 12 h and then removed). The carcass and family were then placed in a new breeding chamber to ensure that no new larvae arrived at the carcass.

(e) Life-history data

Carcasses were checked morning and evening for larval dispersal, which is the point when all larvae cease eating, crawl away from the crypt and remain off the carcass. At the time of dispersal, we recorded the numbers of larvae that survived from a family and these larvae were individually washed, dried and then weighed to within 0.01 mg. Larvae were housed in individual rearing chambers ($8 \times 8 \times 3.5$ cm) filled with 2 cm of soil. We checked the rearing chambers daily and recorded the timing of larval pupation and eclosion. We also recorded the survival to different life-history stages. Overall, this provided us with four measures of offspring performance [26]: (i) duration of larval stage on the resource (time between arrival on the carcass and dispersal), (ii) final larval mass, which is virtually identical to adult size as larvae do not feed after dispersing, (iii) duration of the prepupal wandering phase (time between dispersal and pupation), and (iv) the duration of the pupal phase (time between pupation and eclosion as an adult). We recorded offspring survival as a direct measure of fitness.

(f) Statistical analysis

A multivariate generalized linear model (multivariate analysis of variance (MANOVA) with type III sums of squares) that included polyandry (five levels of polyandry; P) and maternal care (two levels of maternal care; M) as fixed effects was used to compare differences in mean offspring performance traits (Y). The mass of the carcass (C) and the number of larvae per family (L) were also included as covariates (complete model: $Y = \alpha + p + M + (P \times M) + C + L$). Univariate ANOVA was used to ascertain which offspring performance traits were responsible for any significant effects in the overall multivariate model. All offspring performance data meet the assumptions of normality and homogeneity of variances across treatments.

The proportion of offspring in each family that survived to larval dispersal and eclosion was analysed using generalized linear models with binomial error structures [37]. The maximal model was constructed using polyandry (five levels) and maternal care (two levels) as the explanatory variables, and carcass mass and the number of larvae placed on the carcass as covariates. Non-significant variables were removed in a stepwise manner to produce the minimal adequate model [37].

MANOVA and ANOVA were performed using SPSS, including power analysis evaluated at 0.80. Generalized linear models with binomial error structures were carried out using R 2.11.1 [37].

3. RESULTS

(a) Effects of maternal care and polyandry on offspring performance

The duration of maternal care (MANOVA, Wilks' $\lambda = 0.514$, $F_{4,212} = 50.057$, $p < 0.001$) influenced offspring

performance but the level of polyandry was not important ($\lambda = 0.970$, $F_{16,648.308} = 0.409$, $p = 0.981$, power = 0.210) and there was no interaction between treatments ($\lambda = 0.966$, $F_{16,648.308} = 0.457$, $p = 0.966$, power = 0.235). The mass of the carcass ($\lambda = 0.841$, $F_{4,212} = 10.058$, $p < 0.001$) and the brood size ($\lambda = 0.892$, $F_{4,212} = 6.423$, $p < 0.001$) influenced offspring performance. Using univariate ANOVA to analyse significant overall effects, we found that overall performance was better if there was full care, independent of mating treatment. The duration of the larval stage on the carcass was shorter when offspring received only 12 h of maternal care ($F_{1,226} = 19.277$, $p < 0.001$; figure 1a) and these larvae were lighter at dispersal ($F_{1,226} = 138.133$, $p < 0.001$; figure 1b). Among offspring that received only 12 h of maternal care, the duration of the prepupal wandering stage ($F_{1,226} = 57.191$, $p < 0.001$; figure 1c) and the pupal stage ($F_{1,226} = 8.716$, $p = 0.004$; figure 1d) was also shorter. However, independent of treatment, there was a positive relationship between the larval mass at dispersal and the duration of offspring development ($\beta = 18.97 \pm 2.98$, $t_{1,226} = 6.37$, $p < 0.001$). As heavier larvae develop into larger adults [26], this suggests that there was a trade-off between development and adult body size. Offspring that developed on heavier carcasses attained a greater mass at dispersal ($F_{1,226} = 28.297$, $p < 0.001$). Carcass mass was positively related to the prepupal wandering stage ($F_{1,226} = 3.783$, $p = 0.053$) and negatively to the pupal stage ($F_{1,226} = 10.235$, $p = 0.002$). Brood size positively influenced the mass that offspring attained at dispersal ($F_{1,226} = 20.806$, $p < 0.001$).

(b) Effect of maternal care and polyandry on offspring survival

The proportion of offspring that survived to dispersal and eclosion was significantly influenced by the duration of maternal care (at dispersal $F_{1,223} = 5.849$, $p = 0.016$; at eclosion $F_{1,225} = 7.463$, $p < 0.001$). Among offspring that received only 12 h of maternal care, survivorship was lower when compared with those that received maternal care until dispersal from the carcass. There was no effect of the level of polyandry on offspring survival at dispersal ($F_{1,222} = 0.843$, $p = 0.360$) or eclosion ($F_{1,223} = 0.062$, $p = 0.803$). Similarly, the interaction between the duration of maternal care and the level of polyandry had no effect on offspring survival at dispersal ($F_{1,221} = 2.259$, $p = 0.134$) or eclosion ($F_{1,221} = 0.243$, $p = 0.622$). Offspring that developed on heavier carcasses had increased survival to dispersal ($F_{1,223} = 5.036$, $p = 0.026$) but there was no effect on survival to eclosion ($F_{1,222} = 2.842$, $p = 0.093$). Similarly, offspring from larger broods had increased survival at dispersal ($F_{1,223} = 5.164$, $p = 0.024$) and, marginally, at eclosion ($F_{1,224} = 3.739$, $p = 0.054$). Large broods probably facilitate access to the carcass for all larvae in the brood.

4. DISCUSSION

In systems where male traits or behaviour do not allow females to identify their ideal mate, females may use post-copulatory processes to selectively use the sperm from multiple mates to increase the genetic quality of their offspring [1]. In this study, we found no evidence of indirect benefits for polyandrous females. Consistent

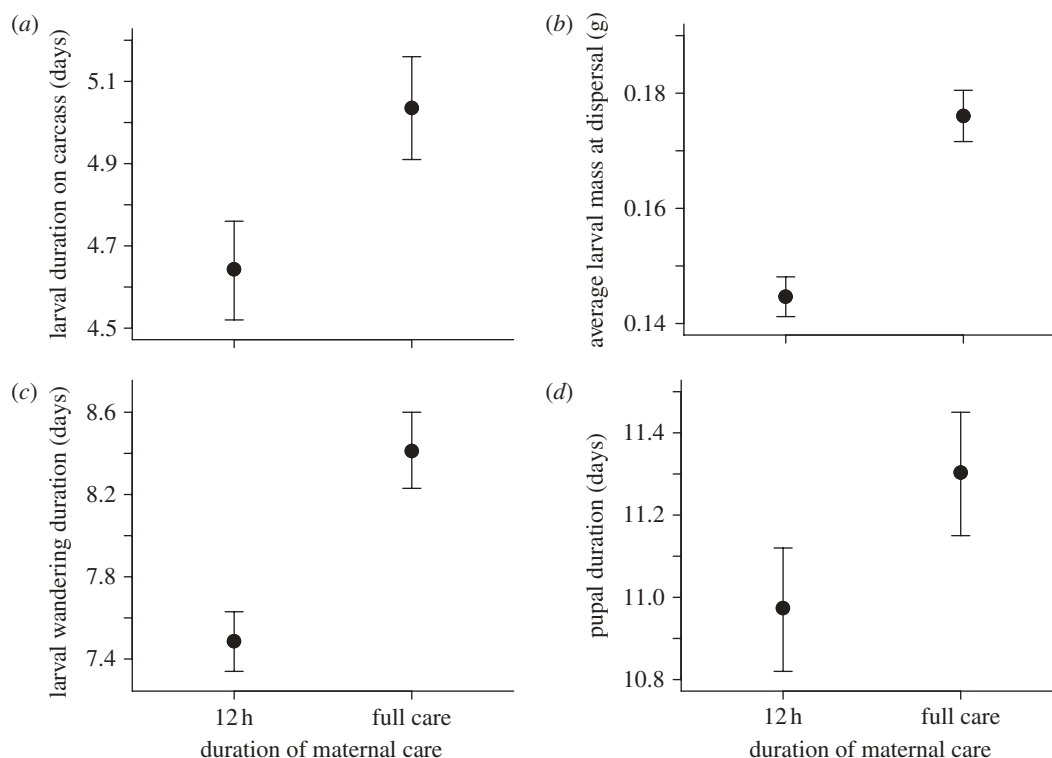


Figure 1. Effects of the duration of maternal care on specific offspring performance characters associated with fitness [26]. (a) Larval duration on the carcass (days), (b) larval mass (g) at dispersal, (c) larval prepupal wandering duration (days), and (d) pupal duration (days). Data are average values \pm 95% confidence intervals for females that provided 12 h or full care for their offspring, regardless of the polyandry treatment that did not influence offspring development.

with other studies, we found that the benefit of maternal care to offspring depends on the duration of the care but contrary to our prediction there was no indication that maternal effects amplify indirect benefits of polyandry, and therefore there was no interaction between maternal effects and level of polyandry. Combined with our previous studies [24–32], we have no evidence that the evolution of high rates of mating in *N. vespilloides* reflect direct or indirect benefits.

Evidence for indirect benefits of polyandry have been found primarily in insects, in particular cricket species [9,38–43]. This may simply reflect the relative ease with which insects are manipulated, but studies of less tractable systems also provide some suggestion that indirect benefits have important implications (e.g. vertebrates [44–49]). It is possible, however, that the influence of polyandry on offspring performance is often mediated by maternal effects and previous studies have confounded maternal contributions with indirect benefits [3]. This occurs if females that mate with attractive males invest more in their offspring through maternal effects. The problem is that maternal effects can be difficult to identify. In *N. vespilloides*, we can distinguish between postnatal maternal effects and indirect benefits by manipulating the amount of investment in offspring following hatching. If polyandry increases the opportunity to mate with preferred or compatible males and therefore post-copulatory mate selection, we might have expected increased maternal investment at more extreme levels of polyandry. In the absence of an effect of varying the levels of polyandry, we find no evidence that females invest more in maternal care depending on the characteristics of their mating partners, or perhaps this adjustment

is trivial relative to the overall effects of care. Furthermore, although indirect benefits of polyandry are often found in the pre-hatching viability of eggs [3,15], there is no evidence of indirect benefits influencing egg viability in *N. vespilloides* [34]. This argues against polyandry in *N. vespilloides* providing females with a mechanism to produce genetically superior, more genetically diverse or more genetically compatible males, because all these hypotheses predict an improved average performance of offspring.

In contrast to the level of polyandry, the duration of maternal care had a strong effect on offspring performance and survival. We show that a longer duration of maternal provisioning increased the mass that larvae attained at dispersal and the likelihood that offspring survived. Heavier larval mass is advantageous even though the larval and pupal stages were longer as heavier larvae are ultimately larger adults that have a competitive advantage in contests for mates [31,33,50] and resources that are required for reproduction [51,52]. Experiments in other burying beetles, manipulating the amount of care, have shown that care positively influences larval growth and development [24–26,30,53]. Thus, while a positive effect of maternal provisioning is unsurprising in this study, it may explain why such strong effects overshadow any indirect benefits of polyandry.

It is of course possible that polyandry is important for female *N. vespilloides* under different environmental conditions, albeit not related to maternal effects [7]. However, support for environment-specific indirect benefits is inconclusive in studies where the levels of polyandry are manipulated and the offspring are reared under variable conditions. For example, polyandrous female frogs (*Crimia*

georgiana) do not benefit from polyandry in any environment [54] and polyandrous female decorated crickets (*Grylodes sigillatus*) produce heavier sons independent of the environment [40]. It appears that the optimal mating strategy of the female yellow dung fly (*Scathophaga stercoraria*) and red flour beetle (*Tribolium castaneum*) are influenced by the environment experienced during early development and that only females producing offspring under certain conditions gain indirect benefits [55,56]. Further investigations are required to determine whether the costs or benefits of the mating change under variable ecological conditions and therefore whether the form and strength of selection for polyandry is temporally and spatially variable [7,57,58].

The question of whether polyandry is adaptive has received considerable empirical attention but the evidence is mixed [1,3]. Under our experimental regime, we show that female *N. vespilloides* do not receive indirect benefits from polyandry. However, absence of evidence is not evidence for absence and we cannot rule out the possibility that indirect benefits exist. *Nicrophorus vespilloides* mate at extraordinarily high frequencies; thus, it is possible that our levels of polyandry were insufficient to detect a benefit [40]. Furthermore, in this system where reproduction is dependent on a limited resource, there are a number of scenarios where females may receive indirect benefits from polyandry. For example, genetically diverse broods may have higher survival by using a carcass more completely by reducing sibling competition or are more resistant to pathogens and parasites. However, given our results thus far [24,32], the most parsimonious explanation for polyandry in *N. vespilloides* is selection for promiscuity in males and the positive genetic variance between male and female mating frequency and speed [32]. The processes that maintain this correlation are unknown but it would appear that the cost of mating is minimal or that mating confers a benefit to females, which reinforces this genetic correlation.

The authors thank John Hunt, Trish Moore, four anonymous reviewers and Howard Rundle and Nigel Bennett for excellent comments. NSF (International Postdoctoral Fellowship to B.H.B.) and NERC (to A.J.M.) supported this work.

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